THE ABILITY OF TWO INTERNAL CLOCK MODELS TO PREDICT PERFORMANCE ON A TEMPORAL BISECTION PROCEDURE.

A thesis

Submitted in partial fulfilment

of the requirements for the degree

of

Masters of Applied Psychology

at

The University of Waikato

by

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2015

Abstract

This research is a replication of Machado and Keen (1999) procedure which tested the ability of two competing models of animal timing; Learning to Time (LET) and Scalar Expectancy Theory (SET), to predict pigeons performance on a temporal bisection task. Hens were trained in two temporal discriminations; in Type 1 trials they learned to choose a red key after a 1-s signal and a green key after a 4-s signal and in Type 2 trials they learned to choose a green key after a 4-s signal, and a yellow key after a 16-s signal to receive access to reinforcement. After they learnt these discriminations, intermediate durations were presented. The resulting psychometric function did not superpose, violating the scalar property of timing. When novel key and duration combinations were presented, performance on subsequent generalisation tests closely matched LET's predictions. Overall, the results support the findings of Machado and Keen (1999) and supported LET's rather than SET's predictions.

Acknowledgements

I would firstly like to thank my extremely patient supervisors Dr. Lewis A. Bizo and Dr. James S. McEwan for their support and guidance. I think you both believed in me far more than I believed in myself and for that I thank you. Thanks to Rob Bakker and Allan Eaddy for their technical support with my experiment, for saving documents that I forgot to back up and for the laughs. Thank you to Jenny Chandler for all your help and support with my experiment, data analysis, for the chocolate and for allowing me to name my chickens after musical theatre characters (without judgement). How else could I keep myself entertained throughout the many many months of running the experiments. Hopefully I paved the way for more behavioural/thespian students who also need that Broadway mix to get them through their thesis.

I would like to acknowledge the other master's thesis students, who ran my experiments but more importantly became part of my university family, thank you for sharing the laughs, the tears and the shared Sigmaplot frustration. I would especially like to thank Surrey Jackson for all your work proofing my thesis; you definitely got me through the final stages of this process. Thank you also to Grace Peel, Fernanda Potgieter, Karmen Ngatai, Zach Penman and Sinead Bicknell for all your support and your belief that this was something I could achieve.

Finally to all my family and friends, I want to say thank you for your unwavering support throughout my academic career. I especially want to thank my parents, to my mum, it has been through your journey wtih Parkinson's that has taught be how to be brave, courageous and to just keep going, you are a true inspiration. Thank you also to my dad; thank you for your steadfast support and belief in me, there is absolutely no way I could have done this journey without your love and

guidance in every possible way. Thank you to my sister, the best big sister a girl could ever ask for, you have taught me to follow my dreams no matter how hard they may seem, what a beautiful lesson. Lastly, thank you to my extremely patient partner. Andrew, thank you for always being there, for your support, for your love and for everything you have done to get me to this stage. I cannot tell you how much I appreciate everything you do.

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Chapter One: Introduction

Animal behaviour occurs in time; to identify a discrete behaviour at some point in the life of an animal is to say when the behaviour begins, and when to say the behaviour has come to an end. Armed with accurate descriptions of animal behaviour that reliably identify these events, we can measure the time that elapses during the performance of the discrete behaviour. By reference to a timekeeping device, we can record which events occurred before and which occurred after the behaviour. We can also record events that occur simultaneously with the behaviour, and articulate the temporal order in which each behaviour occurred. Animal behaviour, defined by Skinner (1938), is differentiated from the lower biological functions and reflexes as something animals do contingently, and not of physiological, chemical, or physical necessity. Behavioural psychology is the science concerned with functional or causal relations to be found between animal behaviour and environmental stimuli. To understand the behaviour of an organism is to understand its learning history, immediate environment, and environmental history gaining insight in order to predict or control future consequences.

The duration and timing of animal behaviour is integral to the successful performance of that behaviour. To the extent that an animal contingently behaves, the animal behaviour involves timing; and to have successfully behaved is for the animal to have timed the behaviour amongst other things. Usually, saying that a behaviour was "timed" by the animal is simply to say that the animal successfully behaved in a certain way. For example, to have caught a mouse, is for the animal to have timed its behaviour successfully. So time is part of the successful behaviour.

Research into animal timing, has been grounded in the correspondence between the timing, the successful performance of the behaviour and the use of human convention to describe the temporal properties of that behaviour. The question remains, what is the functional relation between physical time (measured using human convention) and the animal's subjective time? From an evolutionary perspective, it makes sense that an animal's subjective time should be accurately scaled to physical time (temporal scaling), and that it should accurately distinguish time periods (temporal sensitivity). For it is within physical time that the animal lives, interacts and adjusts behaviour based upon the properties of its environment.

Behavioural research has informed our knowledge on timing, typically these experiments have used stimuli to assess generalisation and discrimination(Vieira de Castro, Machado, & Tomanari, 2013). An essential component of any stimulus is said to be its duration, sharing exteroceptive properties with other stimulus dimensions including wavelength, intensity and sound (Vieira de Castro, Machado, & Tomanari, 2013). Research on timing has specifically focused on the way in which, behaviour adjusts to temporal periodicities in the environment, the causal relationships between timing and antecedent events and the temporal sensitivity required for schedule induced responding (Castro et al.2013).

Timing models

Two early models of timing in animals, one grounded in the methods and insights of cognitive psychology, and the other grounded in the methods and insights of behavioural psychology, have been developed. The first model, Scalar Expectancy Theory (SET), developed by Gibbon (1977), is built upon Weber's

law and the scalar property of time. The theory posits the existence in the animal of an internal control mechanism that regulates the temporal properties of the behaviour in the animal. Although the mechanism itself is unobservable, the model generates falsifiable hypotheses. The second model, Learning to Time (LeT), an associative account of temporal learning is built upon behaviourist assumptions, and a methodological aversion to explaining psychological phenomenon by reference to internal mechanisms. Rather, the functional relations, in this case, especially between an animal's learning history and its successful timing behaviour, are emphasised.

The Scalar Expectancy Theory (SET)

SET became a prominent model in explaining the temporal sensitivity of animals (Wearden, 1991). SET attempted to explain the body of research that was being produced on timing ability in rats and pigeons (Wearden, 1991). Historically, temporally regulated behaviour was first observed by Pavlov in the 'Inhibition of delay' paradigm named 'classical conditioning (Rescorla & Solomon, 1967) but gained far more traction after the development of operant conditioning . SET developed as an extension of Weber's Law (Gibbon, 1991) which described what difference in magnitude was required for two stimuli to be judged as different the (just noticeable difference JND). Weber's Law stated that when expressed as a proportion, the difference in magnitude remained the same across a range of absolute magnitudes (Gibbon, 1991). This was captured mathematically as the Weber fraction which is assumed to be constant, and when it holds is what produces the Scalar property of timing which is said to be a ubiquitous property of timing models (Gibbon, 1991).

Primarily SET was used to describe the phenomena that occurred in timing experiments when choice behaviour was conditional on the availability of reinforcement after an individual response, the latency of response, or an entire sequence of responses such as the Fixed Interval (FI) schedule of reinforcement (DeCasper & Zeiler, 1977). The FI schedule required that a subject be reinforced only after fixed amount of time. This produced a pattern of responding that would shift from a low to a high rate in anticipation of the stimulus occurring, at roughly two thirds of the interval (Wearden, 1991). This produced a 'scallop like distribution named 'a break run pattern'(Wearden, 1991). Timing was also observed in more complex FI experiments, for example, reinforcement being contingent for either pecking a key after 30-s or 240-s after the commencement of the trial. Trials occur randomly with the subject having no indication as to which schedule will be presented. During the long trials, average response rate increases from the beginning of the trial until approximately 30-s has elapsed, gradually decreases, and then increases again at the end of the trial (Catania, 1970; Roberts, 1981) To anticipate the moment in which reinforcement becomes available (i.e. timing two durations simultaneously) is theorised to demonstrate temporal sensitivity.

SET has been used to describe the performance in the Peak Procedure, an extension of the FI schedule developed by Catania (1970). This procedure is an extension of the FI schedule and has also been utilised to asses an animal's ability to produce timed intervals (Roberts, 1981; Sanabria & Killeen, 2007). The procedure consists of two types of trials (i.e. 'normal' and 'peak' trials) which occur within the experimental session with random probabilities of 0.8 and 0.2 respectively (Machado, Malheiro, & Erlhagen, 2009). In the normal trials,

reinforcement is contingent on responding after the presentation of a stimulus, whereas, in peak or extinction trials, responding is not reinforced and the stimuli is terminated (Machado et al., 2009). In this procedure, the 'peak' time or 'peak' rate of responding refers to the maximum time that response rates were at their maximum (Machado et al., 2009). In these trials responding increases until the point at which food would have been delivered on previously reinforced trials causing responding to decreases in an asymmetrical manner with a sharp increase of responding at the latter end of the trial (Machado et al., 2009). Therefore, this anticipation of reinforcement suggests that the animal can accurately predict the point at which reinforcement occurred in the normal trials. (Russell M. Church, Meck, & Gibbon, 1994; P. R. Killeen, Fetterman, & Bizo, 1997; Roberts, 1981).

More recently SET has been used to describe performance in a retrospective timing task, named a temporal bisection procedure which was initially tested with animals (Catania, 1970; Stubbs, 1980) and further employed with humans (Allan & Gibbon, 1991; Wearden, 1991). Typically in this procedure two stimuli differing only in duration (typically four times longer than the first) are mapped onto two contrasting stimuli (Machado et al., 2009). For example, in a double bisection task the subject is exposed to two sample durations, either 1-s or 4-s and 4-s or 16-s, and then chooses between two side keys, lit red or green, or blue and yellow (Machado et al., 2009). If the duration is 1-s, the subject is required to pick red, if the duration is 4-s the subject will pick green, 4-s the subject will pick blue and 16-s yellow (Machado, 2009). Once the subject has gained fluency and is able to discriminate between the four durations correctly at a specified threshold, intermediate durations are presented and stimulus generalisation is examined by measuring the preference (Machado, 2009). The

point of bisection, where the animal perceives both durations to be of equal measure, is said to occur at the geometric mean of the training stimuli or the square root of the values (Machado et al., 2009).

SET, posits that timing occurs through the possession of a 'discrete' internal clock with the structural component seen in Figure 1. In this model a pacemaker generates pulses with a high variable frequency (Machado, 1997). An accumulator counts the pulses until an event, such as reinforcement occurs. At that moment of reinforcement, SET posits that the numbers of accumulated pulses are stored in the subject's memory. For example, in a temporal bisection procedure, SET predicts that an animal forms two distinct memories, the first is the counts obtained at the end of a short stimulus and the second is the counts obtained at the end of a long stimulus (Machado, 1997). To time an event an animal counts the pulses that are obtained at the end of a stimulus (e.g. pulses generated during the signal Xt) and compares them to the sample duration extracted from short term memory Xs, and the sample extracted from long term memory XL (Machado, 1997). The animal will likely choose the red key when the ratio Xs: Xt is closer to 1:1 than the ratio Xl:Xt, for the duration of the signal just experienced is most similar to the short duration extracted from memory(Machado, 1997). The animal will, conversely, choose the green key when the ratio Xl:Xt is closer to 1:1 than the ratio Xs:Xt, for the duration of the signal is most similar to the long duration extracted from memory (Machado, 1997). The probability of choosing the green key is a function of signal duration and a choice decision based upon the discrepancy between the two ratios (Machado, 1997).

SET hypothesizes that, in a time-based task, an animal will form an expectation of the time between reinforcement and will respond on the basis of

the ratio between the estimation formed by the animal at the time and an overall estimation of the time to reinforcement (Machado, 1997). SET does not assume that the pulses are evenly distributed, and as such anticipates that the counts remembered for equal intervals will vary (Machado, 1997). Furthermore, SET assumes the subject to possess a further capacity to sample a count from its long-term memory at the onset of an event to be timed (Machado, 1997) The animal is also said to be additionally capable of *continuously* comparing the activated long-term memory of the final count in a prior trial with its current count until the end of the interval. The ratio between the sampled and the current count determines the instrumental response and is therefore said to underpin the animal's ability to time, constituting a clock (Machado, 1997).

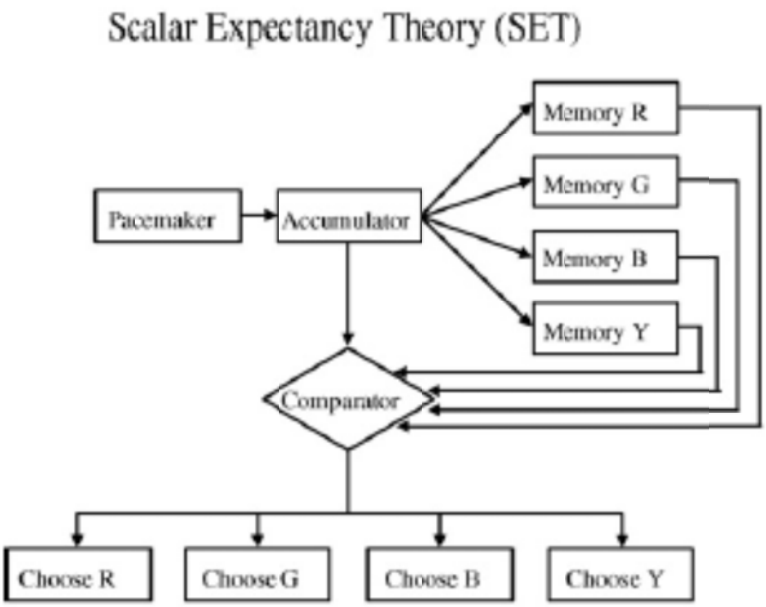

Figure 1. The structure of the Scalar Expectancy Theory (SET) for double bisection procedure. Adapted from "Comparison of Scalar Expectancy Theory (SET) and the Learning-to-Time (LeT) model in a successive temporal bisection task," by J. Arantes, 2008, *Behavioural Processes, 78,* p. 270. Copyright 2015 by Elsevier Limited.

The Behavioural Theory of Timing (BET)

BET proposed by Killeen & Fetterman (1988), posits the existence of an internal clock and pacemaker, similar to SET, yet instead of utilising memory stores, timing behaviour is thought to be mediated by the couplings between behavioural states and responses (Killeen & Fetterman, 1988). BET assumes that behaviour is regulated through a hypothetical pacemaker which transition the animal through a series of behavioural states, with the last activating the operant response (Killeen & Fetterman, 1988).

BET posits that each behavioural state comprises of classes of adjunctive behaviours as catagorised by Staddon & Simmelhag (1971). These behaviours are labelled interim, terminal, emitted or elicited and are based upon where they occur within the (ITI) and their proximity to reinforcement (Lejeune, Richelle, & Wearden, 2006). Overtime, adjunctive behaviours develop into discriminative stimuli (SD) and in turn, aid the animal in making temporal judgements (Killeen & Fetterman, 1988).. Additionally, BET also assumes that these classes of behaviours are correlated with multiple behavioural states and as well as multiple classes of behaviour to a single state (Bizo & White, 1995). The utility of these behaviours as mediating temporal performance as posited by BET has found much empirical support (Fetterman, Killeen, & Hall, 1998; Harper & Bizo, 2000).

Research has illustrated how reinforcement schedules that employ temporal periodicities or constraints including differential reinforcement of low rates (DRL) or Fixed Interval (FI) schedules elicit patterns of adjunctive behaviour (Lejeune, Cornet, Ferreira, & Wearden, 1998). Dews (1972, as cited by Gibbon (1977)) offered a definition of adjunctive behaviour as ‘behaviour occurring between two instances of the responses being studied (or between some

other event and such an instance), which is used by the organism as a controlling stimulus in subsequent behaviours' (p. 729) This phenomenon was first observed in early research, when subjects were exposed to intermittent food schedules eliciting consistent sequences of behaviour (Lejeune et al., 1998). When observed these behaviours consisted of sequences or patterns of natural stereotyped actions (pecking towards the food hopper, cage floor or cage circling) produced within the ITI. (Blaine, Innis & Staddon, 1980; Reberg, Innis, Mann, & Eizenga, 1978; Staddon & Simmelhag, 1971; Timberlake & Lucas, 1985). The utility of these behaviours was also seen to mediate temporal spacing between lever pressing in DRL schedules with rats (Wilson & Keller, 1953) and was also said to increase the accuracy of responding when subjects could engage in behaviours between required responding (Laties, Weiss, & Weiss, 1969).

Although it was apparent that adjunctive behaviours were functional, their underlying temporal contingencies were less understood. Some proponents to their efficacy in aiding temporal cues were proposed by Richelle & Lejeune (1980) in '*Time in Animal Behaviour'*. The authors proposed that if a chain of behaviours were critical in producing an operant response, any restriction or disruption to that chain should prevent subsequent responding, undermining timing ability (Richelle & Lejeune, 1980). The authors also suggested that on visual inspection 'chains of behaviours' were not always evident and at times, stereotypical repetitive like responding of only 'one' behaviour was apparent (Richelle & Lejeune, 1980). Furthermore, in terms of timing accuracy, the authors proposed that those animals who did not engage in any 'observable' adjunctive behaviour were not poorer performers than those who did (Richelle & Lejeune, 1980). Finally, it was suggested that making collateral behaviours contingent on reinforcement, as you

would in pre-training condition, would not necessarily aid in timing acuity (Richelle & Lejeune, 1980).

In response to Richelle and Lejeune (1980), Killeen & Fetterman (1988) proposed that visual inspection of behaviours was sometimes open to disagreement, as the inability to see variations in form and topography could often be due to lack of acuity of the observer (Killeen & Fetterman, 1988). In addition, through the process of conditioning, behaviours were naturally being strengthened by the available reinforcer, independent on whether or not the experimenter could observe the relationship (Killeen & Fetterman, 1988). Furthermore, as adjunctive behaviours naturally develop into discriminative stimuli(SD) they come to serve as accurate predictors of time, this in turn consistutes a clock.(Killeen & Fetterman, 1988). An assumption of BET is that that inter- pulse time is a linear function of the average inter-reinforcement interval (Bizo & White,1994). As the pulses occur with constant probability they produce a Poisson distribution(Bizo & White, 1994).

BET also asserts that the rate of the pacemaker varies with the rate of reinforcement; therefore, if the probability of reinforcement is high, pacemaker rate increases, conversely, if the probability of reinforcement is low, pacemaker rate decreases((Bizo & White,1995). The average time between pulses is a directly function of the inter-reinforcement interval (Bizo & White, 1995). Although it was apparent that adjunctive behaviours were functional, their underlying temporal contingencies were less understood.

In summary, SET offers an account of behaviour on time-based reinforcement schedules through the existence of an internal clock. Pulses produced by an accumulator transition the animal through the passage of time

until an event, such as a reinforcer is delivered. At that point the numbers of accumulated pulses are saved in long term memory for later reference. When a new interval is to be timed, the animal extracts the sample, compares it to the current number in the accumulator and the ratio between the two numbers controls the operant response.

BET also posits the existence of an internal clock and pacemaker system, however, pulses produced by the pacemaker are said to transition the animal through a series of behavioural classes. These behavioural classes, which occur within the ITI, serve as discriminative stimuli for the animal and set the occasion for responding. Therefore, when reinforcement is delivered the animal associates the class of behaviour with the specified response, (i.e. pecking) which in turn, controls the operant response.

The Learning to Time Model (LET)

More recently Machado (1997) offered an account of temporal control which explicitly described the learning process that occurred when subjects were exposed to prolonged schedules of reinforcement. The model posited that the behaviours observed in temporal based schedules were not simply an expression of an internal clock; rather they constituted the clock (Machado, 1997). The Learning to Time (LET) model, a derivative of BET is grounded in behavioural psychology and does not reference any internal mechanisms as an account of temporal control. Rather, the model hypothesises that animals came to regulate their behaviour through a cause and effect relationship with their environment (Machado, 1997). As a model of temporal control LET specifically describes the process that reinforcement and extinction has on shaping behaviour. How stimulus generalisation and discrimination predicts overall responding, and how

behaviour comes to be controlled by time, rather than some other stimulus (Machado, 1997).

The Learning to Time model (LET) comprises of three main structural components as seen in Figure 2. At the top of the structure there is a series or chain of behavioural states (top circles), these states are joined by the associative connections (middle links) which link the behavioural states to the operant responses (bottom circles) and the operant response itself (Machado & Keen, 1999). LET posits that in a time based task an animal is continuously engaged in a series or chain of behavioural states (Machado & Keen, 1999). These states are initiated through the signalling of the availability of food, and are arranged sequentially so the force of each new state activates the next (Machado & Keen, 1999). For example, at the beginning of the trial only the first behavioural state is triggered, and as time elapses, the sequential activation of each new state is generated by the rate and strength of the previous one (Machado & Keen, 1999). Each behavioural state is connected to the operant response; therefore those states highly active at the time of reinforcement become strongly linked to the operant response. Conversely, states that are active when reinforcement is unavailable become uncoupled from the operant response (Machado & Keen, 1999).

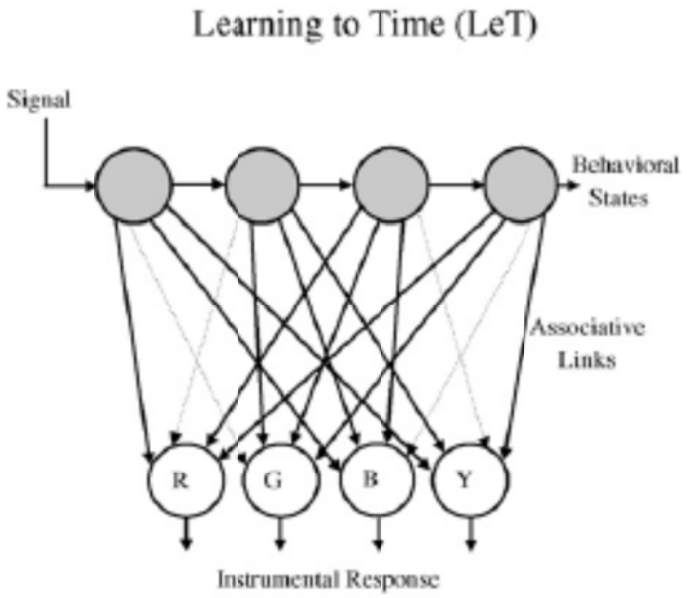

Figure 2. The structure of the Learning to Time Model (LET) for the double bisection procedure. Adapted from "Comparison of Scalar Expectancy Theory (SET) and the Learning-to-Time (LeT) model in a successive temporal bisection task," by J. Arantes, 2008, *Behavioural Processes, 78,* p. 270. Copyright 2015 by Elsevier Limited.

Similar to BET, the behavioural states referred to in the model are variations of adjunctive behaviours, which occur within the ITI, are schedule induced and are said to underpin the temporal regulation of behaviour (Machado et al., 2009). These behaviours and the way in which they mediate the operant response encompass the learning component of the model (Machado & Pata, 2005). For example, states highly associated with food exert more control over those less associated with food (Machado et al., 2009) These associations are said to initially develop in the pre-training and training stages of the experiment and are said to remain relatively robust over time (Machado et al., 2009). In summary, the temporal regulation of behaviour occurs through three fundamental processes; the rate of activation of behavioural states, the process of reinforcement and extinction either strengthening or weakening the operant response and how these processes are mapped onto observable behaviour (Machado et al., 2009). Unlike other models LET negates that animals passively tell the time through some internal mechanism, rather the model posits that behaviour itself becomes the best predictor of time.

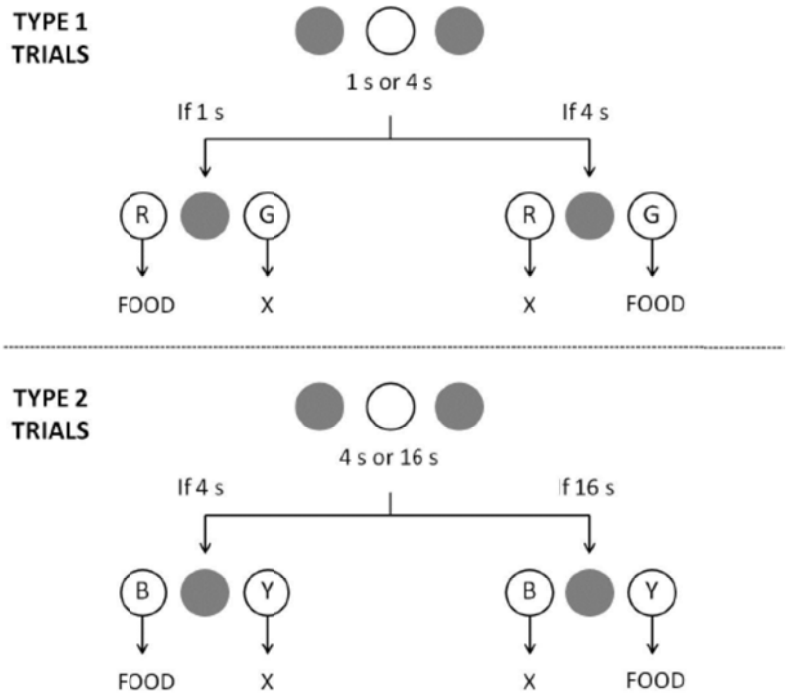

Figure 3. Structure of the two types of training trials in a double bisection task. Adapted from "Context effect in a temporal bisection task with the choice keys available during the sample," by Oliveira, and Machado, 2009, Behavioural *Processes, 78,* p. 287. Copyright 2015 by Elsevier Limited.

To test the predictions of both SET and LET, Machado & Keen (1999) extended the simple bisection procedure so that two discriminations were taught within the same session as seen in Figure 2. For example, in Type-1 trials subjects were trained to choose red after a signal duration of 1-s and green after signal duration of 4-s. In type-2 trials subjects were trained to choose blue after a signal duration of 4-s and yellow after a signal duration of 16-s (Machado & Keen, 1999). After fluency was achieved, both trials were integrated within the same session and stimulus-generalisation and response-generalisation was tested by pairing novel key and colour combinations and assessing preference (Machado & Keen, 1999). Both timing models make varying predictions as to how animals learn to time events, and how this is observed in the psychometric functions (Machado & Keen, 1999). For examaple, it is predicted that the psychometric increases from 0 to 1 as stimulus duration increases also (Machado & Arantes, 2006; Machado & Keen, 1999). The point at which the psychometric function equals 0.5 commonly called the point of subjective equality (PSE), typically tended to occur when the probe durations were equal or close to the geometric mean, a pattern observed in studies with humans (Allan & Gibbon, 1991; Rodriguez-Girones & Kacelnik, 1998; Wearden, 1991) and animals (Russell M Church & Deluty, 1977; Machado & Arantes, 2006; Machado & Pata, 2005; Platt & Davis, 1983; Stubbs, 1980). SET predicted that the psychometric functions derived from both trial types will superpose, whereas LET predicted the line generated by the psychometric function for Type-2 trials will be steeper than that of the function for Type-1 trials (Machado & Keen, 1999).

To further test both models,(Machado & Keen, 1999) investigated what effect novel key combinations had on timing performance after the initial

discriminations were mastered. For example, stimulus-generalisation was tested through the pairing of original stimuli with novel light combinations and stimulus-response generalisation was tested by pairing novel test durations with key-colour combinations (Machado & Keen, 1999). SET predicted indifference between choosing the green and blue keys associated with the 4 second durations in both Type-1 and Type-2 trials respectively when participating in a novel trial combining the green and blue keys (Machado & Keen, 1999). According to SET, as both durations came from identical distributions 'stored' in memory from the original trials the animal would remain indifferent (i.e. context independent) (Machado & Keen, 1999). This indifference is shown by the horizontal line in Figure 3. Whereas, according to LET the animal's preference for the green key will increase monotonically as the signal duration increases, a decision based upon previous associations of other stimulus durations presented in previous trials (i.e. context-dependent) (Machado & Keen, 1999).

This critical test between the blue and green keys is named the context effect has been tested in research conducted by (Machado & Keen, 1999); (Machado & Pata, 2005); (Machado & Arantes, 2006); (Oliveira & Machado, 2008); (Vieira de Castro et al., 2013). Furthermore, as seen in Figure 3, LET predicts a U-shaped function when both the red and blue keys are presented simultaneously, whereas SET predicts a decreasing psychometric function producing a similar pattern of responding to those observed with novel stimuli (Machado & Keen, 1999).

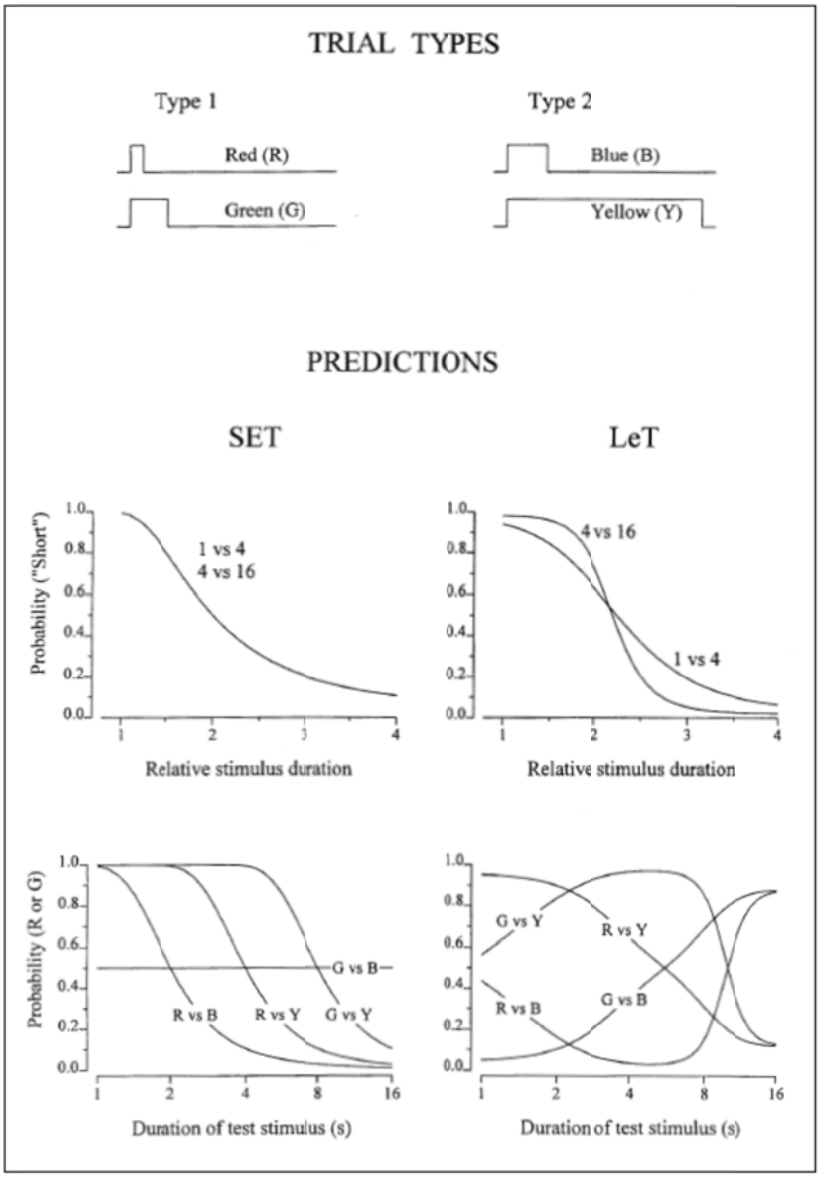

Figure 4. The structural of the double bisection trials (top panel), predictions of both SET and LET with previously trained durations of Type 1 and Type 2 trials (middle panel) and novel combinations (bottom panel). From "Learning to Time (Let) or Scalar Expectancy Theory (SET)? A Critical Test of Two Models of Timing" by A. Machado and R. Keen, 1999, *Psychological Science, 10*, pp. 287. Copyright 2015 by Sage Publications Inc. Journals.

SET predicts memory storage occurs after the delivery of a reinforcer and as the animal 'counts' each pulse generated by the pacemaker, what is stored in memory is a number that represents the duration of the interval (Staddon & Higa1999). This means that the contents saved in an animal's memory remains the same irrespective of the rate or availability of reinforcement; extinction plays no role in SET (Staddon & Higa, 1999). Whereas in LET, reinforcement and extinction will either strengthen or weaken the couplings between states and their paring with the operant response (Staddon & Higa1999). This means LET predicts stronger connections between behavioural states and the operant response when the rate of reinforcement increases (Staddon & Higa1999). Finally, SET predicts an animal will have access to all information throughout the duration of the trial, allowing memories to be sampled continuously (Staddon & Higa, 1999). In contrast, LET predicts an animal will only have access to relevant information when each successive behavioural state becomes active.

Machado & Keen's (1999) empirical results failed to definitively support the assumptions of either theory, or reject the hypotheses drawn from the theoretical assumptions of either timing model. Neither model could predict the occurrence of the bisection point substantially below the geometric mean reported in the original paper. However, the results from the stimulus generalisation and stimulus response generalisation tests in the original experiment did not support SETs predictions as the psychometric functions did not overlap, whereas LET only failed to accurately predict the data from the stimulus generalisation conditions.

My first aim in this research is to replicate Machado and Keen's (1999) experiment, critically testing two competing models of the phenomenon of timing

in animals - namely, Learning to Time (LET; Machado, 1997) and the Scalar Expectancy Theory (SET; Gibbon, 1977). My second aim in this research is to test the hypotheses generated by the two competing models of timing and determine whether the empirical evidence generated by replicating Machado and Keen's (1999) experiment contradicts the hypotheses of either theory.

Chapter Two: Methodology

Subjects

Three domestic Barneveld hens numbered 10.1, 10.3 and 10.6 and three Crossbreed Bantam roosters numbered 10.2, 10.4 and 10.5 (all *Gallus domesticus*) participated in the experiment. The hens had prior experience pecking response keys for food and had previously been in experiments with basic schedules of reinforcement. The roosters had no prior experience pecking response keys for food. All birds were approximately two years of age at the start of the experiment. They were housed individually in wire cages that were approximately 430-mm high x 500-mm wide x 450-mm deep in a ventilated room lit on a 12-hr light and 12-hr dark cycle. All birds were maintained at 80% ± 5% of their free-feeding body weight, maintained by post-session feeding of commercial pellets. All birds had free access to water in their individual cages, with grit and vitamin supplements provided on a weekly basis.

Apparatus

An experimental chamber, which measured 615-mm long x 450-mm wide x 580-mm high was used. The interior of the chamber was white with three keys and a food magazine mounted on the right hand side of the chamber. The food magazine was located behind an opening (115-mm high x 70-mm wide) and centered 105-mm above the floor and lit by a 1-W light bulb.

Each response key was a frosted transparent Perspex key measuring 30-mm in diameter, positioned 390-mm from the floor and 85-mm apart in a horizontal position and could be lit by either a red, blue, yellow, green or white 28 –V multi-chip LED (light-emitting diode) bulb. The force required to activate the key was approximately 0.1N and key activation was signalled by an audible beep. When

activated, a light above the magazine was illuminated and the magazine was raised to allow access to reinforcement (wheat grains). All experimental events were controlled and recorded from a computer running MED-PC IV software.

Procedure (Training)

At the start of each training phase a bird was placed into the chamber. The centre key was illuminated with a white light for a duration of either 1, 4 or 16-s and signalled the beginning of the trial. After the signal duration elapsed, two keys either side of the centre key were illuminated with either a green and red or blue and yellow light, arranged on left and right keys and responses were recorded. During the training subjects were taught two discriminations. In Type 1 trials the two sample durations were 1-s and 4-s. At the end of the sample duration two keys on either side of the centre key were lit red or green randomly. If the sample duration was 1-s the subject selected red to obtain reinforcement and if the duration was 4-s the subject selected green to obtain reinforcement. Therefore, when the sample durations were 4-s and 16-s and the side keys were lit either blue or yellow, with blue being associated with the 'short' duration and yellow associated with the 'long' duration. On Type 2 trials when the sample duration was 4-s the subject selected blue and if the duration was 16-s the subject selected yellow. Trials were separated by a 20-s inter-trial interval (ITI), correct choices were reinforced, and incorrect choices were not reinforced and the trial was repeated.

Training consisted of four conditions. In the first condition all birds were trained on Type 1 trials until all could discriminate between both sample durations with 80% accuracy across repeated trials for ten consecutive days. Once this was achieved all birds were trained in Type 2 trials with the same criteria as above. In

the third condition all birds were presented with Type 1 and Type 2 trials across alternate days for a period of 8-38 days depending on individual accuracy and finally in the fourth condition, both Type 1 and Type 2 trials were presented in the same session across 10-20 days. After all birds had completed the training and after achieving 80% accuracy across 10 consecutive days, the experiment proper began.

Experiment proper

Condition 1: Regular plus extinction trials

Condition 1 was in two stages. In stage one, Type 1 and Type 2 trials were incorporated into the first 10 sessions; correct responses were reinforced, whereas incorrect responses lead to the repeat of the trial. In stage two of this condition, extinction trials, approximately 10 sessions, were introduced. In the extinction phase of the trial, correct and incorrect responses did not lead to reinforcement and incorrect responses did not result in the repeat of the trial. Sessions comprised of 72 trials of which 48 were regular trials where correct response were reinforced and 24 were extinction trials.

Condition 2: Stimulus generalisation trials.

In this condition, there were 48 regular trials and 24 stimulus generalisation trials interspersed throughout the session. Over the course of these two trial types, two sets of logarithmically spaced durations were used to test stimulus generalisation. For Type 1 trials; 1.41, 2 s, and 2.83 s and for Type 2 trials; 5.66s, 8 s and 11.31 s. The middle duration of the test durations corresponded to the geometric mean of the training stimuli. The test stimulus generalisation trials (test trials) occurred four times in a session and was presented

on both left/right key colour combinations. Stimulus generalisation trials (test trials) were never followed with reinforcement.

Condition 3: Regular plus extinction trials.

This condition was identical to the first condition and lasted 5 sessions in total.

Condition 4: Response generalisation trials.

This session comprised of 56 regular trials and 24 response generalisation trials. For both sets of trials the stimulus durations remained constant (e.g., 1 s, 4 s & 16 s), with the exception of response generalisation trials, where four new pairs of colour combinations were presented. These new combinations were R-B, R-Y, G-B, and G-Y, whereas in previous trials the colour combinations were always R-G and B-Y, due to this change, there were 12 unique combinations of response generalisation trials. Each unique combination occurred twice per session, and lasted for 20 sessions.

Condition 5: Regular plus extinction trials.

This condition was identical to the first condition and lasted for a maximum of five sessions. The only difference in this condition was an increase in extinction trials from 24 to 32.

Condition 6: Stimulus-response generalisation trials.

In this last condition each session comprised of 56 regular trials and 32 test trials. The signal duration during the test trials alternated between 2 s and 8 s long and was paired with R-B, R-Y, G-B, or G-Y choice colour combinations. The 8 test trials were presented four times within each session and were presented twice for each left key/right key colour combinations. This condition lasted for 16

sessions. During this condition an intermittent key light problem was discovered, caused by a loose wire; therefore all animals were put back on baseline for 10 days, data from the effected condition was discarded and replaced with data from the repeated conditions.

In conclusion, the first, third and fifth conditions were used to maintain the basic discriminations and minimise any carryover effects caused by previous training and conditions. Condition 2 tested for stimulus generalisation using the same colour keys whilst altering durations. Condition 4 tested for response generalisation by using novel colours and normal durations, and Condition 6 tested for response generalisation with both novel colours and durations.

Data collection

Data collection included the number of responses made to the left and right keys during the choice phase of each trial. Responses were recorded separately for all trial types. Data recorded was the proportion of responses to the left and right key/colour combinations. The total session time, number of trials completed and reinforcers obtained on Type 1 and Type 2 trials were recorded also.

Table 1. *A breakdown of all pre-training and training conditions, consisting of reinforced trials, extinction/probe and test trials.*

	Condition	Trial Types	Total Trials	Reinforced trials	Extinction/ Probe Trials	Test Trials	Days 10.1	Days 10.2	Days 10.3	Days 10.4	Days 10.5	Days 10.6	
ii	Pretrain	Type 1	48	48	n/a	n/a	16	13	13	9	9	10	Pretraining
ii	Train	Type 1	48	48	n/a	n/a	26	26	19	16	12	20	Type 1
iv	Train	Type 2	48	48	n/a	n/a	18	20	18	17	14	26	Type 2
v	Train	Type 1 & 2 alternate days	48	48	n/a	n/a	8	20	24	21	27	38	Alternate session
vi	Train	Type 1 & 2 within session mixed	48	48	n/a	n/a	18	16	20	11	10	10	Same session
1a	No extinction trials		48	48	n/a	n/a	11	15	12	0	10	9	Condtion 1 part 1
1b	Extinction trials	Type 1 & 2 mixed	72	48	24	n/a	10	11	10	20	11	11	Condition 2 part 2
2	Duration	Type 1 & 2 mixed	72	48	24	Duration	10	10	13	19	11	19	Condition 2 - Stimulus generalisation trials
3	Baseline	Type 1 & 2 mixed	72	48	24	n/a	13	10	10	11	15	12	Condition 3 - Regular plus extinction trials
4	Colour	Type 1 & 2 mixed	72	48	24	Novel colours	31	34	34	22	29	27	Condition 4-Response generalisation trials
5	Basline	Type 1 & 2 mixed	82	48	32	n/a	16	15	15	13	15	14	Condition 5 - regular plus extinction trials
6	Colour and duration	Type 1 & 2 mixed	82	48	32	Novel colours/ durations	53	55	54	52	57		Condition 6 - stimulus response generalisation trials

Chapter 3: Results

Stimulus Generalisation

Figure 1 shows the individual data for all birds for Condition 2, for the stimulus generalisation experiment, when the probability of choosing the short stimuli was plotted against relative stimulus duration for both Type 1 and Type 2 trials. The sample durations on the long tests were plotted as a function of relative duration, allowing both trials to be plotted together on the same axis. The data indicates that when subjects chose the shorter response for each trial type, the psychometric function derived from the data decreased monotonically as signal duration increased. Furthermore, inspection of the curves for the individual birds, show a clear failure of superposition as the functions for the two sets of stimulus durations do not overlap. For all birds, the curves for the 4 vs.16s trials tend to be steeper than the curves for 1-s vs. 4-s trials, with the exception of bird 10.1 where the psychometric functions show less separation.

The failure of superposition was also confirmed from the results of the fits from the logistic equation and represented by the smooth lines and data points. Table 1 shows for individual animals, the means and standard deviations of the psychometric functions shown in Figure 1. Paired t-tests confirmed the failure of superposition, as both the means and standard deviation, reported in Table 1, for 1-s vs. 4-s trials were statistically significantly larger than for the 4-s vs. 16-d trials, $t(5) = 3.98$, $p = .005$, and $t(5) = 2.30$, $p = .034$ for means and standard deviation, respectively. Lower Weber fraction equals high discriminability and produces a steep psychometric function whereas; the higher weber fraction equals lower discriminability and produces a shallower psychometric function. For five

out of six subjects the Weber fraction was lower for 4 vs. 16-s then for 1 vs. 4-s. In addition for five out of the six subjects the psychometric functions were steeper.

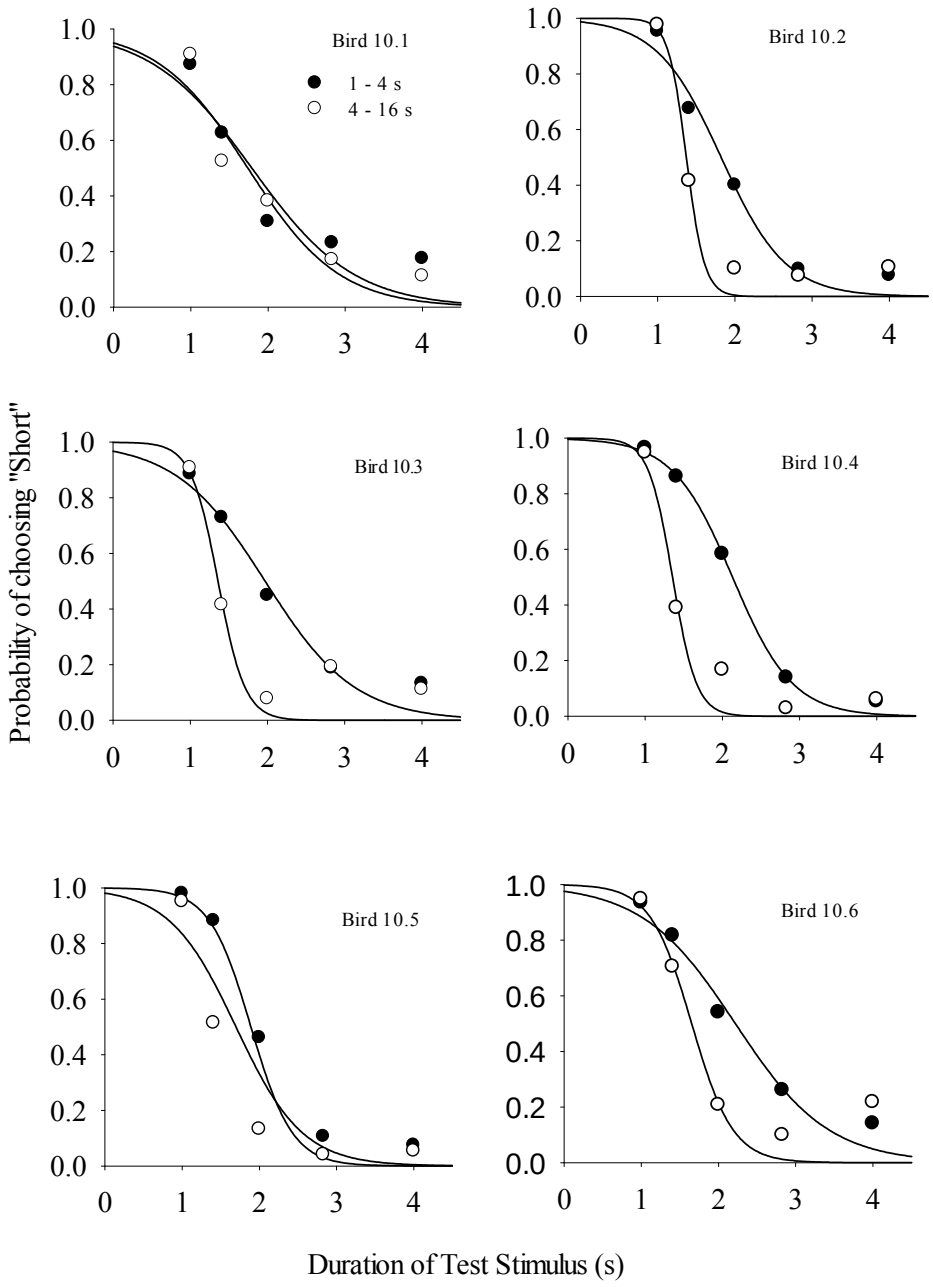

Figure 5. The proportion of 'short' choices during stimulus generalisation test trials for all 6 birds. The filled circles correspond to Type 1 trials and the open circles correspond to Type 2 trials. The data is collected from all sessions in Condition 2.

Table 2. *The mean, standard deviation, variance and standard error of the estimate and the Weber Fraction of the psychometric function for all birds for Type 1 Trials (1 vs. 4) for Condition 2.*

Type 1 Trial 1 vs. 4	Hen		$\overline{X}$	σ_X	σ^2	σ_{est}	Weber Fraction
	10.1		1.792	1.198	0.866	0.126	0.669
	10.2		1.823	0.758	0.976	0.068	0.416
	10.3		1.970	1.053	0.968	0.069	0.535
	10.4		2.132	0.704	0.997	0.027	0.330
	10.5		1.890	0.489	0.996	0.033	0.259
	10.6		2.218	1.095	0.971	0.068	0.494
		$\overline{X}$	1.971	0.883	0.962	0.065	
		σ_X	0.172	0.274	0.049	0.035	

Table 3. *The mean, standard deviation, variance and standard error of the estimate and the Weber Fraction of the psychometric function for all birds for Type 2 Trials (4 vs. 16) for Condition 2.*

Type 2 Trial 4 vs. 16	Hen	$\overline{X}$	σ_X	σ^2	σ_{est}	Weber Fraction
	10.1	1.740	1.072	0.904	0.114	0.616
	10.2	1.372	0.214	0.957	0.092	0.156
	10.3	1.360	0.317	0.889	0.132	0.233
	10.4	1.355	0.282	0.949	0.991	0.208
	10.5	1.697	0.784	0.942	0.103	0.462
	10.6	1.653	0.486	0.899	0.136	0.294
	$\overline{X}$	1.529	0.526	0.923	0.261	
	σ_X	0.185	0.337	0.029	0.358	

Response Generalisation and Stimulus-Response generalisation

Response Generalisation and Stimulus-Response Generalisation trials consisted of the total number of sessions for Condition 4 and 6 respectively. Response generalisation was tested by presenting novel key colour combinations (R-B, R-Y, G-B, and GY) with previously experienced test durations, yielding twelve novel test trials. Stimulus response generalisation was tested by pairing 2-s and 8-s signal durations followed by a choice of R-B, R-Y, G-B or G-Y colour combinations. Figure 2 shows the individual results for all birds from the combined response generalisation and the stimulus-response generalisation trials when the short response was plotted as a function of stimulus duration.
For all six birds the top left hand panel shows the probability of choosing G when the choice between G and B is presented with the 4-s stimulus duration. For all birds, as stimulus duration increased, preference for choosing G increased also. The bottom left hand panel shows that when presented with the choice between R and Y, paired with 1-s and 16-s respectively, preference for R decreases as stimulus duration increases.

The top right hand panel shows the probability of choosing R when the choice between R and B is paired with the 1-s and 4-s duration. Although there were slightly individual variations, the results showed a U like pattern, which shows an initial preference for red decreasing and then increasing at the latter end of the trial. Finally, the bottom left hand panel shows the probability of choosing G when the choice between G and Y is paired with the 4-s and 16-duration. The result show the preference for G increases with signal duration and then decreases rapidly.

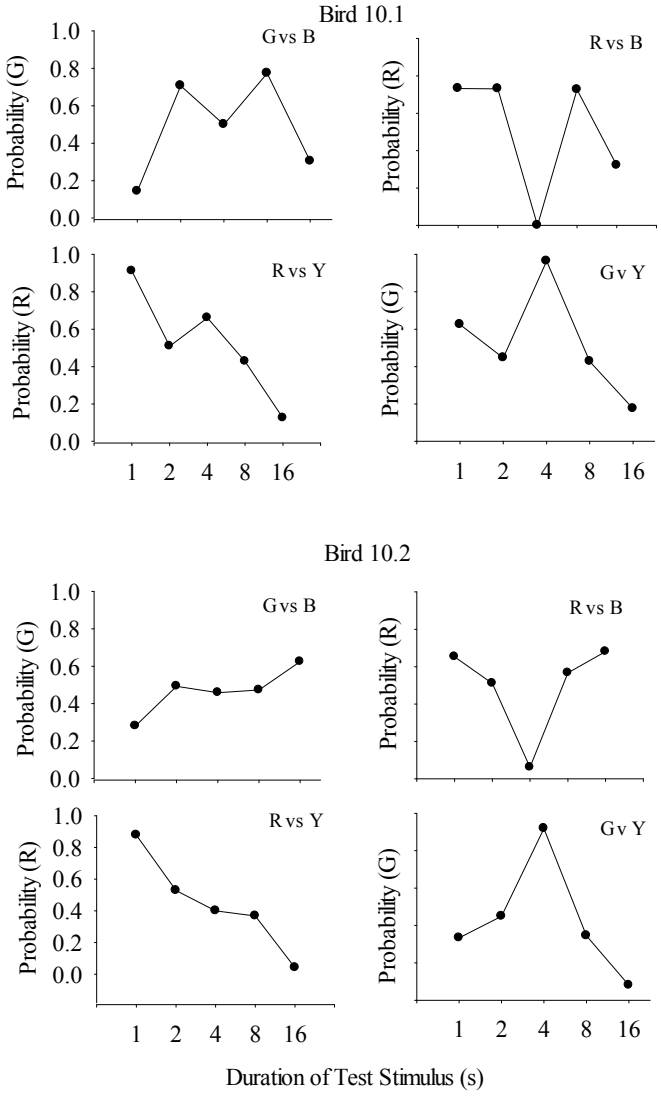

Figure 6. The individual results for 10.1 and 10.2 when the proportion of choices is plotted as a function of stimulus duration for Type 1 trials. (i.e. red, R, or green, G). Each individual graph corresponds to a new key combination. Data was collected from all sessions of Condition 4 and 6. The logarithmic scale on the x-axis B=blue key, Y=yellow key.

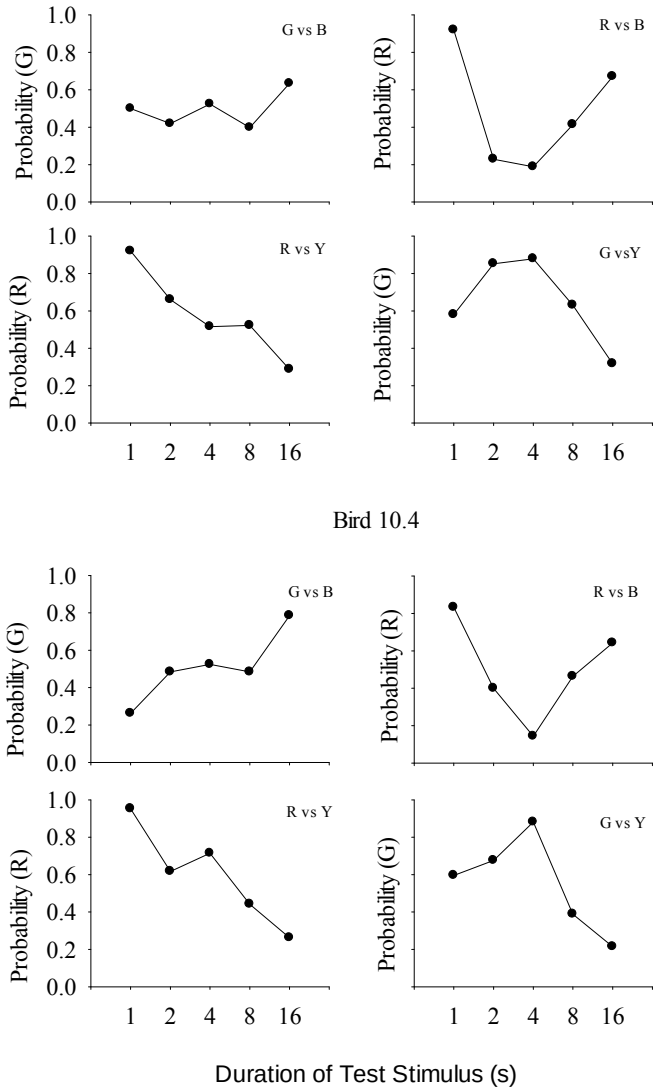

Figure 7. The individual results for 10.3 and 10.4 when the proportion of choices is plotted as a function of stimulus duration for Type 1 trials.

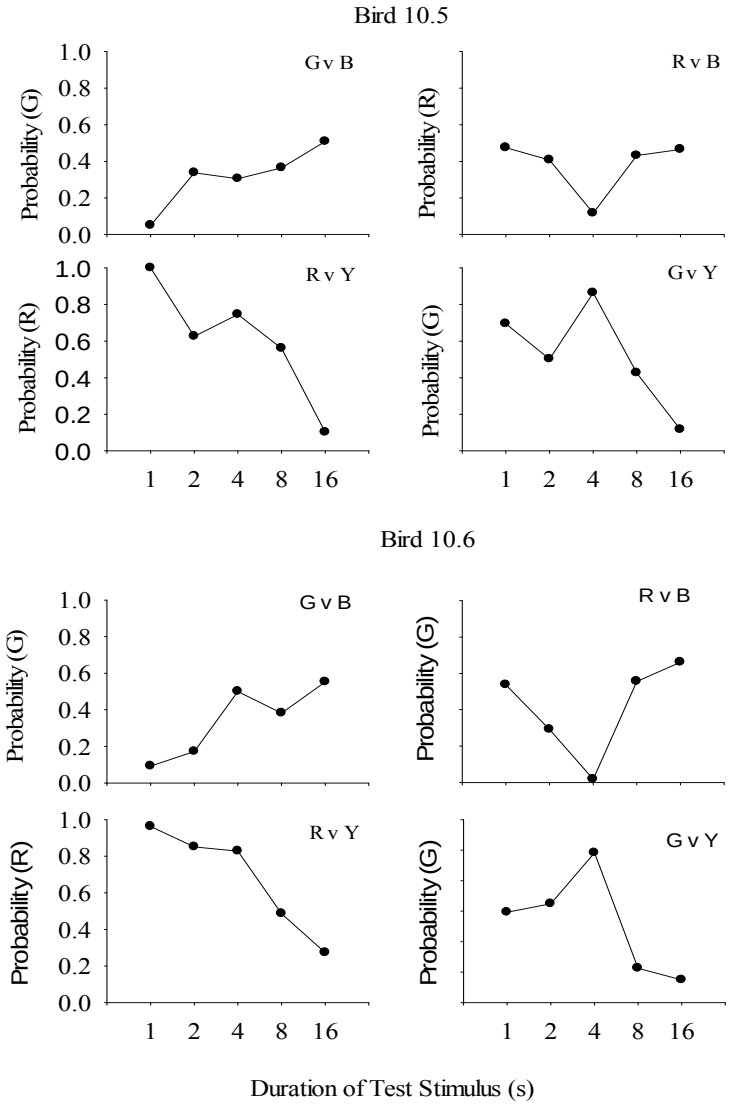

Figure 8. The individual results for 10.5 and 10.6 when the proportion of choices are plotted as a function of stimulus duration for Type 1 trials.

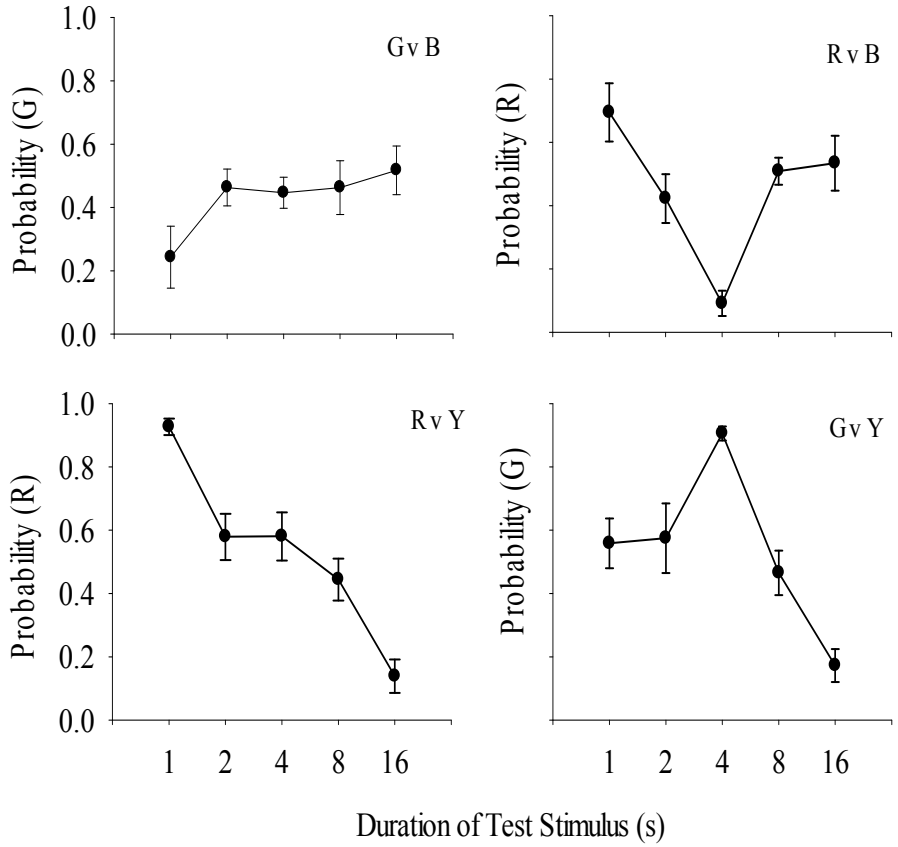

Figure 9. The averaged proportion of choices for all birds for Type 1 trials (i.e., red, R, or green, G) as a function of stimulus duration. Vertical bars show the standard error of the mean. Data was collected from all sessions of Condition 4 and 6. The logarithmic scale on the x axis. B=blue key; Y= yellow key.

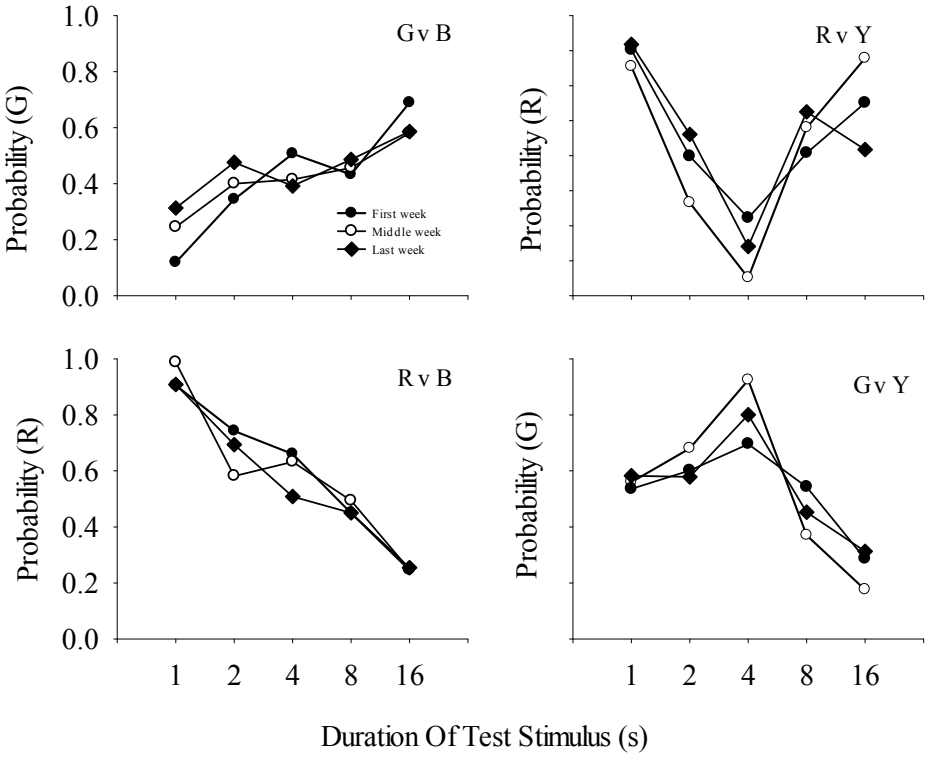

Figure 10. The averaged proportion of choices for all birds for Type 1 trials (i.e. red, R, or green, G) as a function of stimulus duration for the first, middle and last seven days of the combined results for Conditions 4 and 6. The logarithmic scale on the *x* axis. B=blue key; Y= yellow key.

As all birds showed a similar pattern in responding for the *stimulus response* and *stimulus generalisation trials*, the results were averaged proportion of choices from Conditions 4 and 6 for all birds from Type 1 Trials (R & G) as a function of stimulus duration. In Figure 2.1 each of the four panels refers to the novel key combinations and the error bars refer to the standard error of the mean, namely the standard deviation of the sample means estimate of the population mean. Results are as follows, when G and B are paired (4-s stimulus) for all birds, as the test duration increased, the probability for choosing G also increased. When R is paired with Y (1-s stimulus vs. 16-s stimulus) the probability for choosing R decreases monotonically as stimulus duration increases. When R is paired with B (1-s vs. 4-s), preference for red increases and then decreases in a u-like pattern. . Finally, when G and Y are paired together (4-s vs. 16-s) the probability of choosing green increases up until 4-s then decreases rapidly as the stimulus duration increases.

The result replicate Machado and Keen's (1999) study, however, at the 8-s mark LET predicts a preference for green, and conversely SET does not predict the initial increase for green at the beginning of the trial. The results from the combined response generalisation and stimulus-response generalisation trials show that performance was relatively consistent across all birds and did not alter with repeated experience in those conditions. Figure 2.2 reports the results of the data of the averaged proportion of choices from condition 4 and 6 for all birds from Type 1 Trials (red & green) as a function of stimulus duration for the first, middle and last seven days of the condition. The results indicate that even after prolonged exposure to the condition, performance of all birds, remained relatively unchanged across time.

In summary the results show that for the *stimulus generalisation* trials, the resulting psychometric function did not superpose, violating the scalar property of timing. When novel key and duration combinations were presented for the *response generalisation and stimulus-response generalisation* and performance on subsequent generalisation tests closely matched LETS predictions. Overall, the results support the findings of Machado and Keen (1999) and supported LET's rather than SET's predictions.

Chapter 4: Discussion

This research contributes to the increasing range of experiments that are using double temporal bisection procedures to compare and contrast two competing models of the phenomenon of timing in animals - namely, LET (Machado, 1997) and SET (Gibbon, 1977). The present study replicated the same procedure used by Machado and Keen (1999), whom investigated timing ability in pigeons using a variation of the temporal bisection procedure (Machado & Arantes, 2006; Machado & Keen, 1999; Machado & Pata, 2005). The specific aim of this research was to test the predictions generated by the two competing models of timing to determine whether the empirical evidence produced by replicating Machado and Keen's (1999) experiment contradicted the hypothesis of either theory.

Stimulus-generalisation

In Experiment 1 for the stimulus-generalisation trials, both SET and LET made contrary predictions regarding the form of the psychometric function when the two trial types (e.g., discriminations) were presented within the same session. When the probability of choosing the short duration was plotted as a function of relative stimulus duration for both trial types, SET predicted the superposition of both psychometric functions in relative time (Machado & Keen, 1999). SET is built upon Weber's law and the scalar property of time (Gibbon, 1977). Weber's Law states that when expressed as a proportion, the difference in magnitude remains the same across a range of absolute magnitudes (Bizo, Chu, Sanabria, & Killeen, 2006). Weber's Law states that Weber fractions will remain consistent when given a constant short duration to long duration ratio. This study had a constant short duration to long duration ratio of 1:4 between both type one and

type two trials (Bizo, et al. 2006). The results of this study were that for five out of six subjects the Weber fraction was lower for 4 vs. 16-s then for 1 vs. 4-s. In addition for five out of the six subjects the psychometric functions were steeper. Other studies utilising temporal bisection procedures, have also found a failure of Weber's Law to predict deviations in the Weber fraction at longer duration ranges for example (Bizo, et al., 2006; Lavoie & Grondin, 2004; Zeiler & Powell, 1994).

Conversely to SET and Weber's law, LET predicted the psychometric functions for Type 1 and Type 2 trials would not superpose, and the psychometric function for Type 2 trials would be steeper than that of the function for Type 1 trials (Machado & Keen, 1999). As 5 out of 6 birds yielded steeper psychometric functions for the Type 2 trials, a violation in the superposition effect was found. The failure of superposition was also confirmed statistically with the fits from the logistic equation shown in Figure 5. The flatter psychometric function produced by the shorter duration gives further support for LET and is comparable to Machado and Keen's (1999) results.

As Weber's Law and the Scalar Property of Time fundamentally underpin SET any deviations in these predictions aid in invalidating the theory as an account of temporal control. It is essential that the underlying core assumptions of any theory be confirmed in the research. If not, further investigation as to why the theory cannot adequately account for the data is required. LET proposes the steepness in function for Type 2 trials is directly related to the specific behaviours being performed at the time at which the subject makes the choice decision (Machado & Keen, 1999). For example, as trial length increases the probability of behaviours being under the control of the 'long' duration also increase. Therefore, once the subject is engaged in 'long' behaviours it is less likely they will be able

to return to performing behaviours that have been associated with the short duration (Machado & Keen, 1999). The results from the present study, for the stimulus generalisation tests give support to role adjunctive behaviours have in temporal discrimination.

Response Generalisation and Stimulus-Response Generalisation

In Experiment 2, response-generalisation and stimulus-response generalisation were tested by introducing novel colour and key combinations with previously experienced durations and assessing preference. A critical test of both models was seen when the two durations (e.g. green and blue) both associated with the 4- second signal duration were presented simultaneously during a novel trial combination (Machado & Keen, 1999). The models made opposing predictions on the form of the psychometric functions as well as the underlying learning assumptions, namely the context effect. Predictions made by SET assume that when subjects enter the experimental stages of the trial, all discriminations have been mastered (Vieira de Castro et al., 2013). SET also assumes that when presented with both stimuli (i.e. green and blue), both associated with the 4-s stimulus duration, the subject will remain indifferent to the duration just experienced (Vieira de Castro et al., 2013). This is grounded in the assumption that both durations come from independent identical distributions stored in memory and are available for recall (Castro, et al., 2013). Furthermore, as the subject has learnt each duration independently, recall does not rely on the 'context' of neither alternate durations being presented nor any associated behaviours. Temporal learning is attained, independent of context (Castro, et al., 2013)

Conversely, when presented with both signal durations, LET predicts that the animal's preference for the green key will increase monotonically as the signal

duration increases. This pattern of choice is clearly illustrated in both the results in Machado and Keens (1999) research as well as the present study. The inability of SET to account for this pattern of responding is said to be attributed to the way in which discriminations are learnt which is represented within the structural mechanics of the model (Arantes, 2008).

For each discrimination learnt by the subject, SET posits that a separate memory of each duration (1 vs. 4 s) and (4 vs. 16 s) is stored and is available for retrieval throughout the trial (Arantes, 2008). When the subject is presented with the previously unpaired durations with the requirement to pick 'short' or 'long', the subject compares the durations with those previously experienced and selects accordingly. (Arantes, 2008). When the two keys both associated with the 4-s signal duration (e.g. blue and green) were presented simultaneously, SET failed to predict the curve of the psychometric function which showed the preference for the green increasing monotonically as signal duration increased. According to SET the results should show indifference to either duration shown by the superposition of the two psychometric functions (Arantes, 2008).

Conversely to SET, LET predicted a very different choice decision when subjects were presented with both green and blue keys simultaneously. For example, in the pre-training and training stages of the experiment when subjects were presented with the 1-s signal duration and chose green, responding was not reinforced. This ensured that any associations formed between the green key and behavioural states expressed at the time of reinforcement were weakened (Vieira de Castro et al., 2013). Similarly, when subjects were presented with the 16-s signal duration and chose blue, responding was not reinforced and associations between the blue key and behavioural states expressed at the time of

reinforcement were also weakened (Vieira de Castro et al., 2013). Due to this process the subject was therefore more likely to select the 'blue' key after the presentation of 1-s signal duration and the green key after 16-s signal duration. The choice decision is therefore determined by the context of other durations presented within the trial. This critical choice illustrates a robust account of the context effect which has been reproduced in research Arantes, (2008). The context effect cannot be derived by the current assumptions of SET. This is because SET assumes the independence amongst temporal memories associated with the keys (Machado & Arantes, 2006). This result therefore, casts doubt on the ability of SET to account for temporal discrimination within a temporal bisection procedure.

The results from the other key colour combinations also follow Machado and Keen's (1999) study with LET accounting for both learnt associations and the form of the psychometric function. One point of interest in this study was whether or not performance would change after repeated exposure to the stimuli. As all subjects were exposed to the final condition (i.e. Condition 6) for a total of fifty days comparisons were made for this first, middle and last seven sessions of the condition. All data was averaged and the results clearly showed that performance remained relatively stable across time for all subjects. This result would suggest that any early associations formed between stimuli through the process of reinforcement and extinction, in the pre-training and training stages of the experiment. This pattern of responding was maintained throughout all conditions, producing a robust pattern of responding that did not alter as a function of experience.

In summary the results from the stimulus generalisation trials showed that the results psychometric functions did not superpose, violating Weber's Law and

showing that the Scalar Property of time is not ubiquitous as some have claimed. Furthermore, for the critical choice, when novel key and durations were presented for the response-generalisation and stimulus-response generalisation trials, performance closely matched LETs predictions, further validating an account for the context effect. Furthermore, when performance was measured across the first, middle and last seven days of the final condition, responding remained relatively stable and did not alter as a function of experience.

Mediation of behaviour

Unlike Machado and Keen (1999) this present study did not extend to observing the birds within the operant chamber. This therefore limited the current studies capacity to predict and describe possible correlations between psychometric functions obtained and their relationship to temporal categorisation of adjunctive behaviours. At the essence of LET is the assertion that behaviours are not merely an expression of the inner runnings of an internal clock, rather behaviours essentially function as the clock (Machado, 1997). Moreover, sequences of adjunctive behaviours differentially associated to the operant response are assumed to underpin timing accuracy (Machado, 1997). To confirm the validity of LET as comprehensive account of temporal control, observations of adjunctive behaviours within the current research, would have been fortuitous.

Theorists positing roles in the mediation of behaviour have conducted numerous studies built upon the observations of Staddon and Simmelhag (1971), the classification of adjunctive behaviours and their role in timing performance. Theorists grounded in a behavioural approach have tried to illustrate the efficacy of these behaviours as a timing strategy. Although much of the literature has taken a conservative approach in inferring a causal relationship between the two, their

role has been well documented. Killeen, et al., (1997) illustrated the role adjunctive behaviours had in a retrospective timing task, by analysing the errors that occurred within the trial. It was hypothesised that if behaviours were a cue for subsequent responding then an 'incorrect choice' should be correlated to an 'incorrect behaviour' performed. Killeen, et al., made a frequency distribution of adjunctive behaviours executed at the beginning, middle and later end of the trial (e.g. standing on the left or right hand side of the chamber, packing or pecking on the key). Results clearly showed that when subjects were classifying signal durations incorrectly; they were either performing long behaviours when required to choose 'short' or 'short' behaviours when required to choose 'long'. Furthermore Killeen, et al., reported that they observed distinct behavioural patterns which correlated to opposing signal-durations, and could classify specific behaviours in real time.

To further illustrate the efficacy of adjunctive behaviours and their role in timing performance, Fetterman, et al., (1998) utilised a retrospective timing task using two species (e.g., rats and pigeons). The experiment was broken up into two separate stages which consisted of spatially-differentiated and colour-differentiated-response tasks (Fetterman, et al., 1998). The results were varied. On the spatially-differentiated task, pigeons were trained to discriminate between two sets of durations (short vs. long) for both easy (6 vs. 12 s) and difficult (6 vs. 9s). Observers coded the behaviours performed during the trials and inter-observer agreement was at 85% reliability. Behaviours performed by the subjects when asked to choose short or long, were plotted on a graph as a function of time, shown in Figure 2. A distribution of the probability of engaging in adjunctive behaviours performed on the spatial discrimination task for the easy

discrimination (top row) and difficult discrimination (bottom row) was plotted as a function of time (Fetterman, et al, 1998). What emerged from the data was a pattern of adjunctive behaviours that were duration specific for both discriminations.

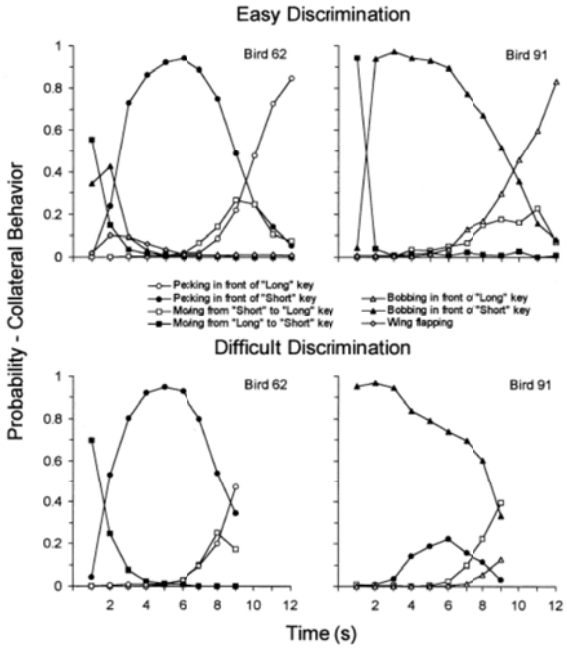

Figure 11. The probability of engaging in collateral behaviour as trial length increases for two pigeons , trained to discriminate 6 from 12s (top row) and 6 from 9 s (bottom row) for a left to right key response. Adapted from "Watching the Clock", by G. Fetterman, P. Killeen and S. Hall, 1998, *Behaviour processes, 44*, p. 13. Copyright 2015 by Elsevier Limited.

More recently, Killeen and Pellón (2013) discussed the relationship between reinforcement and the acquisition and maintenance of adjunctive behaviours. The authors suggested through the process of instrumental conditioning, derived through proximity to reinforcement and respondent conditioning, derived through associations formed including signalling stimuli, adjunctive behaviours naturally become operants. The authors noted three important characteristics of schedule induced behaviour including "its excessiveness, temporal location and dependency on inter-food interval length"(p. 18). These characteristics can strengthen associations between varying modes of a behavioural system and either inhibit or reinforce subsequent responding (Killeen & Pellon, 2013).

General conclusion

All behaviour occurs in time as a particular kind of process or event in the world; namely a vital process in the life of an animal. Skinner (1938) differentiates the category of animal behaviour from the lower biological functions and reflexes, as being a contingent occurrence - not a physiologically, chemically, or physically necessary, occurrence in the life of the animal. Hence our understanding of behaviour as such invokes the representation of time: what we are observing when we observe an animal behave is something that has a definite duration – a discreet beginning and an end. The duration of the behaviour is something that human beings can employ conventions and devices to time precisely, and in this way relate the duration of the behaviour back to the objective duration, physical time. But clearly human conventions have little to do with the ordinary lives of animals and the physical environments in which traits evolve and adapt in a population, and in which animals learn and develop. The

survival and reproduction of the animal in its natural environment depends upon the correspondence of the animal's subjective timing and the objective passage of time.

Psychological theories provide us with competing answers to the question *how* it is that animals are able to track the passage of time and coordinate their overt behaviour successfully in reference to other processes and events occurring in time. Animal behaviour under controlled experimental settings provides researchers with the raw data needed to confirm or invalidate the hypotheses generated by these theories. The fundamental interest of the research question and the rapid development of experimental psychology as a field of scientific inquiry has seen research into timing in animals flourish in recent years, which deepens our understanding of animal behaviour. The results of this research fall in favour of the behaviourist approach, but the question is not yet settled. Further research particularly into the role of adjunctive behaviours in animal timing, and more ethological studies into timing behaviour in its natural setting will enrich our understanding of this fundamental feature of animal behaviour.

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Appendix A

Excel files with a summary of raw data are attached on the accompanying CD.

Appendix B

Ethics approval (protocol number: 894) is attached on the accompanying CD.